RESPONSES OF VENUS FLY TRAP (DIONAEA MUSCIPULA) TO FACTORS INVOLVED IN ITS ENDEMICST

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INTRODUCTION

Probably the first mention of Dionaea muscipula was under the name of “Catch Fly Sensitive” by Governor Dobbs of Brunswick, North Carolina in letters to Peter Collinson of England in 1759 and 1760 (Harper 1942). In the letter of April 2, 1759 Dobbs said, “We have a kind of Catch Fly Sensitive which closes upon anything that touches it. It grows in this latitude 34 but not in 35°." It was John Bartram of Philadelphia (King’s Botanist) who first sent specimens to Collinson in 1763 (Darlington 1849). These were passed on to Ellis and Solander, along with other North American plants for study. The excitement with which Collinson received Dionaea is expressed in a letter to Bartram dated May 10, 1763 in which he said, ... “Think my dear John, with what amazement and delight I, with Doctor Solander, surveyed the quire of specimens ...” But what surprises us most, is the Tipitwitchet3 Sensitive. It is quite a new species, a new genus. It was impossible to comprehend it from any description, which made me so very impatient to see it.” Ellis recognized its affinity with Drosera, but since the material was dried he was unable to comprehend the sensitive mechanism until William Young brought living material to England in 1768. Then, in 1769 in a letter to Linnaeus, Ellis wrote the first botanical (Latin) description of Dionaea which he published in 1770 together with a colored plate (Fig. 1).

Dionaea, a monotypic genus within the family Droseraceae, is endemic to the central southeastern coastal plain of North America, and has, since its discovery, stimulated botanists and naturalists to much investigation, discussion, and speculation, particularly concerning the nature and action of the leaf. The important contributions to knowledge of Dionaea up till 1942 were thoroughly reviewed by Lloyd in his book on “Carnivorous Plants.” Since then only a few papers on Venus fly trap have appeared.

The unique characteristics of Dionaea are widely known among botanists and have made it the subject of a great diversity of studies. Rather surprisingly it has been given no attention, in terms of endemism or senescence, by phytogeographers but this neglect may be related to the general lack of information on its ecological responses and requirements. No orderly study of Dionaea from this point of view has ever been attempted. Only cursory and incidental descriptions of its habitat and ecological characteristics are available. Thus it was with the hope of con-

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3 “Tipitwitchet” was the name by which Bartram and Collinson knew Dionaea until the time when Ellis named it.
The limited following information during Governor Meager's term indicated that the flowering racemes are too long and that the terminal flower always opens first, rather than the proximal laterals.

Contributing to the understanding of the ecology of the species that the present study was initiated.

Range and Distribution of Dionaea

Since the discovery of Dionaea muscipula by Governor Dobbs its range has been somewhat ill-defined, with the general consensus being that it is limited to an area around Wilmington, North Carolina. This misconception was dispelled in 1928 when Coker published a map of its range, as accurately as known at that time, and discussed briefly the locations given by various collectors.

To supplement Coker's report, a list of all Dionaea specimens in 19 American herbaria was obtained together with whatever information, often extremely meager, that appeared on each label. Then an attempt was made to relocate as many as possible of the reported stations. In addition, much time was spent searching for unrecorded stations, especially during the flowering season when the plants are most easily noted. Personal contacts with botanists, naturalists and farmers provided much supplementary information and led to several new records.

The field and herbarium search indicated that the species is much more widely dispersed in some areas than expected and in others is more restricted. It soon became apparent that human activities and absence of fire are very important in restricting the occurrence of Dionaea.

As to reported range limits, the most northern station near Chocowinity in Beaufort County was probably very nearly relocated (Fig. 2), but even this station has since been demolished by the erection of a sawmill. It is likely that careful search in the vicinity, particularly during the flowering season, would turn up more plants, because there are numerous localities here which appear to be favorable for them.

The southern limit on the Santee River (Charleston County, S. C.), based on a report by General C. C. Pinekney, was unconfirmed at the time of Coker's paper, but a new location was found there in 1949 by Bell (University of North Carolina Herbarium). However, the herbarium label indicated that only 3 plants were seen at the site. Although our search in the area in 1956 failed to verify its continued presence, it is probable that a more extended exploration would confirm it, particularly as there are numerous apparently favorable habitats in the vicinity, fire seems to be fairly frequent, and agricultural development is at a minimum.

The western limit seems fairly well established in Moore County, but farming practices of that region have probably brought about its extinction as it could not be relocated though every effort was made to do so. It was relocated in the Fayetteville area, but the erection of a Ball Park on this site suggests its imminent disappearance from here as well.

The accompanying map (Fig. 2) gives the distribution of the plant as inferred from herbarium material, and confirmed by observations during the course of this work. The herbarium locations are marked by open circles, the relocated areas by double circles and the new stations by black circles. Specimens from all newly reported stations have been deposited in the Duke University Herbarium. The main difference between Coker's map and the one given here is in the general limits of the range. Coker does not show any location south of Georgeville, S. C., but gives a location in Wayne County, N. C. No evidence has been found in field work or from herbarium specimens to support this latter observation.

Apparently, as Coker and earlier writers believed, Dionaea muscipula is not doomed to extinction in North and South Carolina, but its range may be severely curtailed by human interference and land usage. In many undisturbed areas, particularly in Brunswick, New Hanover, Bladen, Onslow and Carteret Counties in North Carolina and in Horry County in South Carolina, great numbers of plants are present over wide stretches of land which are not likely to be used in development. The increasing use of controlled burning by foresters in these areas may contribute to its survival.
**Geology of the Dionaea Territory**

The coastal plain of the southeast was deposited during the late Mesozoic and Cenozoic on a horizontal or gently sloping basement in the Atlantic Ocean. The Pre-Pleistocene sediments are chiefly marine but the origin of later ones is controversial. As many as seven successively younger terraces have been recognized between the Fall Line at about 270 ft elevation and the coast, each presumably marking a marine inundation during an interglacial period. However, Flint (1940) considers only the four lowest of these terraces to be marine, designating the youngest as Suffolk and the next three combined as the Surrey. Richards (1950) considers only the Suffolk to be marine and all the others between it and the Fall Line as mainly alluvial in origin. These latter sediments are, in the main, not fossiliferous or contain only plant fossils (Dr. E. W. Berry, personal communication).

Most of the Dionaea habitats of the lower coastal plain are on the Suffolk and Surrey terraces where the chief sediments are sands. These sands make up the greater part of the derived soil. The Suffolk and the Surrey date from the Sangamon and Yarmouth interglacials (120,000 and 250,000 yrs ago). The age of the superficial sands in Moore County is questionable. The underlying Tuscaloosa formation is a sand of Upper Cretaceous age but the overlying sands, considered to be a relic of former shore lines and forming the sand hill region, are probably Pliocene or Pleistocene. Although the Pleistocene and more recent sediments are mainly sands, silts and
clays of alluvial origin, beach sand is also present, as well as peat accumulations in areas of high water table.

Any ideas on the geologic history of Dionaea, or even of its migration in relatively recent time, must be conjectural. Fossil pollen from bog studies might be helpful but none has been recognized. Nevertheless, the history of the development of the coastal plain invites speculation on the occurrence of Dionaea during this time.

During the Mesozoic and Cenozoic the present sandhills of Moore County presumably were dunes along ancient coastlines much like those along the present south Atlantic coast. If, at that time, there were climates similar to the present, there must also have been habitats like those now existing in the lower coastal plain, including sites where Dionaea could have grown. Such conditions and the occurrence of Dionaea were possible through Pliocene time. With the gradual exposure of the coastal plain during the Pleistocene, migration of Dionaea to the south and east could then have occurred, as suitable habitats became available, and could have continued until the present range was reached. Perhaps the range was once greater than it is today; perhaps the potential range has not yet been attained. The present climate and distribution of habitats suggest that a wider range might be possible but the evidence for a conclusion is inadequate.

FIELD OBSERVATIONS

GENERAL DESCRIPTION OF DIONAEA HABITATS

It cannot be said with any certainty that Dionaea will be found wherever the conditions described below occur, but it can be stated with confidence that the macro-conditions within Dionaea locations are similar over a wide area.

Typically, Dionaea grows in semi-pocosin (or semi-savannah) areas or, where pocosins are limited, in zones around their edges. Thus, it is immediately established that the habitat is intermediate between the wet evergreen-shrub bogs, and the dry sandy regions of the surrounding longleaf pine—wire grass savannahs. Canby in 1868 said of its habitat: "It is somewhat singular that this little herb is only found in the vicinity of Wilmington in North Carolina, and the adjacent parts of South Carolina, where it is comparatively common in the damp rich soil bordering the bogs and swamps." Dean (1892) pointed out, using an area east of Wilmington as an example, that "the plant is not, as often supposed, a native of dry and sandy flats, nor like Drosera, common on moist mud flats, nor yet on the high brinks and plant covered banks of large stagnant pools. It appears to be less general in its actual place of occurrence than the common predatory plants that are well represented in this region." Thus, both workers recognized the ecolonal nature of the habitat, a fact often overlooked by collectors as most herbarium records merely list "savannah" or "bog."

There has been little comment on the nature of the soil. Ellis (1770) described it as "a light black mould intermixed with white sand, such as is usually found on our moorish heaths." Canby's conception of the soil as being "rich" was evidently based on the dark color; it is, in fact, very infertile as will be shown in a later section. No other observations have been recorded on this topic, except that Wells (1932) remarked that the soil "does not become excessively wet or dry."

Frost tolerance is not a trait usually associated with Dionaea, but this has been recognized from the time of its first discovery. Bartram, in a letter to Collinson dated May 1st, 1763, says: "I have one root of the Tipitwitchet. It bears our winters [Philadelphial]—is strong this spring" (Darlington 1849). Canby also pointed out its hardiness and recently Mr. Henry Wright of Highlands, North Carolina, transplanted it to the mountains, where it has survived for several years and even produces flowers every summer. During 1956-57 unprotected plants survived frosts in Durham, N. C. down to 10° and 12°F without any ill effects and continued to grow, though slowly, through the whole winter. No mention of tolerances to hot weather exist except Ellis' comment on the climate of the original location: "Swarms of Carolina, near the confines of South Carolina about the latitude of 35° North, where the winters are short and the summers very hot."

Fire is common in all Dionaea areas, and as a result the ground vegetation is sparse, and the soil often has a "pepper and salt" appearance due to the incorporation of charred and decaying organic material into the white sand. Sometimes there is a shallow layer of peaty material above the inorganic soil. There are no species which are always in association with Dionaea but instead a mixture of savannah and bog types with wide moisture tolerances (e.g. Ilex, Zenobia, Lyonia, Polygala, Liatris, Aristida). Not all of these occur in every location and in different places the proportions vary. However, there are three other insectivorous genera (Pinguicula, Sarracenia, and Drosera) which nearly always occur with flytraps in varying abundance. The land where Dionaea grows is generally completely flat or with less than a 3% slope; where this slope is present, as is usual around a pocosin, populations have quite well defined boundaries: a dense shrub zone at the lower side marks one limit while the other is apparently determined by the summer depth of the water table. Over wide flat areas especially in several of the southeastern counties, Dionaea is distributed throughout large tracts of land which have not been disturbed. It rarely grows in depressions where water is likely to collect, but on the edges of such positions, a fact also noted by Dean (1892). Such hollows which have filled with Sphagnum, sometimes support Dionaea but these are not typical habitats. In the usual site the surface of the ground is generally damp, except that at the upper limit of a population zone it may become completely desiccated to a depth of several inches during the driest part of the year. The
sand in these positions may be almost snow white at the surface due to the lack of organic matter and pleurial action.

Dionaea may at times colonize disturbed areas if competitive growth is at a minimum. It is not uncommon on the right-of-ways of railroads, where vegetation is kept under control by constant cutting or burning. The best example of this type of colonization is along the Atlantic Coast Line Railroad between Wilmington and Jacksonville in North Carolina, as well as Highway US 17 which runs parallel with it for the greater part of its length. Here the soil and water conditions are very similar to the natural type and clearing operations favor good Dionaea development.

**Localities of Specific Field Studies**

Combined with the attempt to relocate all reported stations for Dionaea, begun in the fall of 1954, was a search for habitats with large enough populations in suitable locations for detailed study. Reasonably extensive sites were needed for field experimentation and it seemed desirable that they have fairly distinct boundaries. Because daily observations were anticipated, the location had to be considered. During the summer of 1955 two such localities (Locations 1 & 2) were selected for study. Both were within 16 mi of the Duke University Marine Laboratory at Beaufort, N. C. (Fig. 3).

Location 1 (Fig. 4) was 0.5 mi south of Gales Creek on the west side of N. C. highway 24. It contained two stations (Z1 and Z2) within the Dionaea zones around the pocosins, and satellite station S1 in the savannah between. Location 2 (Fig. 5) was approximately 2 mi further south beside an unnumbered county road to Newport from N. C. 24. The site was about 0.5 mi from N. C. 24, just across a small tributary of Broad Creek and on the south side of the road. Here Station Z3 was set up within the Dionaea zone and satellite S2 in the savannah.

The two locations were similar in outward characteristics. Each was a small sandy savannah surrounded by a horseshoeshaped band of pocosin which was less than 2 ft lower in elevation. Both were representative of many similar areas in the vicinity. Species of *Zenobia, Lyonia, Ilex* and *Smilax* predominated in the pocosins with a few scattered pond pines. The savannahs supported longleaf pine and a ground cover of wire grass (*Aristida stricta*). The ecotone between, marked by the addition of widely spaced, low ericaceous species, was the zone of Dionaea concentration. The longleaf pines of Location 1 were young trees, and very few were present, while those of Location 2 were mature and more abundant. Vegetational analyses and soil borings at both locations provided material for an idealized transect of the relations of the Dionaea ecotone (Fig. 6).

Fire had occurred in both locations during the spring of 1955, but there was no subsequent burning.
velocity is reduced more in the zone area than it is in the savannah.

**TEMPERATURE**

Records were kept of maximum and minimum temperatures from July 1955 to mid-September 1956. The widest range of air temperature (94°F) was observed at a savannah station (S1) where the minimum was 21°F in December 1955 and the maximum was 115°F in July 1956. The widest range (92°F) in a zone (Z1) was from 112°F in July 1955 to 20°F in December 1955. Since 1955 summer records are lacking for the savannah, absolute comparisons cannot be made. However, maximum temperatures in zone stations were slightly lower in 1956 than in 1955. Throughout the observation period air temperatures of both savannah and zone stations were very similar, except during the spring there was never more than 2°F difference in the respective maximum and minimum temperatures. In the spring, however, (end of March to beginning of June), the maximum air temperature in the savannah was up to 14°F higher than the air temperature of the zones.

Soil temperatures of the zone and savannah, on the other hand showed a more marked variation during most of the year, but especially during the spring when differences of up to 20°F between the respective maximum and minimum pairs were recorded. At these times the savannah instruments recorded the higher temperatures. During the summer the maximum soil temperatures in the savannah were seldom below 135°F while the zone maximum soil temperatures fluctuated between 110°-135°F. The ranges of soil temperatures were from 20°F (Dec.)—135°F (summer) in the zones and from 22°F (Dec.)—135°F (summer) in the savannah.

There is probably a definite correlation between the high evaporation rate and the pure sand soil of the savannah and its higher soil temperatures. The soil of the savannah dries out earlier in spring and more completely than the zones so that the savannah soil temperatures show a more rapid increase in the early spring and reach higher maxima.

**PRECIPITATION**

No measurements of precipitation were made because it was assumed that there would be little or no difference between the zone and savannah and conclusive records could not be obtained over a short period.

Within the Dionaea region, and to a distance of 50 mi from the outer limits, U. S. Weather Bureau records of 35 yrs duration or longer, were consulted. Snow rarely falls in this general area, and is more prevalent outside than within the range of Dionaea. During the year, rainfall at any one place is apt to be erratic, particularly during the summer, because of local convectional thunder showers, but over the years these irregularities become smoothed out. The mean precipitation for 12 stations within the Dionaea region was 49.95 in., while 6 stations outside the region had an average of 46.31 in. When precipitation for the
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4 seasons was compared, it was found that the average spring precipitation of both areas is equal, while in each of the other three seasons rainfall is highest inside the Dionaea region. The maximum rainfall of both sets of stations occurs in the summer months (June, July, August), when more than a third of the total precipitation falls. South Carolina stations have higher rainfall than those in North Carolina, but there does not appear to be any general conclusion to be derived from this. Fayetteville and Southern Pines have rainfall totals which are more like coastal than inland records.

**DISCUSSION**

The temperature and evaporation data collected over the 14 month period during 1955-1956 do not indicate very great differences between the Dionaea zone and the surrounding savannah. Although temperatures at one of the savannah stations indicate slightly greater extremes than within the zones, the differences do not appear to be great enough to be directly effective in limiting the zone. It is clear that insolation, as determined by the differences in white and black bulb losses is not important. However, the greater evaporation rates in the savannah as determined by the white bulb data may be of indirect significance when related to other factors.

As shown in the studies of the soil, the depth of the water table increases and the amount of organic matter in the soil decreases progressively from pocoin to savannah, and it is in this aspect that the higher evaporation of the savannah is important in restricting the Dionaea zone. Water loss from the soil is greatly speeded up by the lack of ground cover and the presence of an almost pure sand surface soil, and from the plants, by the physical conditions favoring high transpiration rates. Replacement of water from below is slow and thus since the roots of Dionaea are so short, it is not able to compete successfully with such plants as Aristida.

The study of general meteorological records showed that average precipitation inside the range of Dionaea is slightly higher than outside. However, the difference does not appear to be sufficiently great to be of primary importance in delimiting the region, especially when it is realized that some of the stations just to the south of the range have a higher precipitation than those within the Dionaea area.

Various combinations of temperature were used in an attempt to find some correlation with the boundary, but without success. Studies of the climate within and without the range of Dionaea do not indicate an obvious factor which could be directly responsible for limiting its distribution.

**SOIL STUDIES**

**CLASSIFICATION**

The soils of the southeastern coastal plain included in this study have been developed chiefly from Pleistocene and recent sediments under the influences of a warm temperate climate with moderately high rainfall (50 in.), high ground water table and, to a lesser extent, fire.

The Klej-Leon and closely related soil series occurring primarily in regions of smooth relief, are the chief soils occurring in that region of the coastal plain where Dionaea is found. The chief soil forming the Dionaea substrate belongs to the St. Johns series, a ground water podzol (Lee 1955), as was observed in practically all borings taken at Dionaea sites. The soil profile descriptions for these sites were all very similar; most have a thin layer of peaty material at the surface, with a dark gray or black surface horizon, gradually lightening in colour with depth, overlying a coffee-brown cemented layer—the hardpan. Beneath this, the color varies somewhat from brownish-gray to almost yellow. Occasionally excessive wetness of the strata below 10 in. made it impossible to bring samples to the surface and prevented positive identification of the soil type. Otherwise all soil borings were regularly taken to a depth of at least 30 in.

**PHYSICAL AND CHEMICAL ANALYSES**

The profile of a 5 ft deep soil pit dug at Location 2 showed the characteristic development of the St. Johns series (hardpan soil), with a dark-coloured surface horizon gradually becoming lighter with depth and overlying, in this case, a yellow-brown sand. Plant roots were almost entirely confined to the top 3 in. with the few scattered in the next 10 in. mainly belonging to the various shrub species.

The physical properties were determined using samples from this pit and indicate the typical development of a ground water podzol in this region. In the hydrometer separation of sands, the total sands averaged between 93% and 98% at all depths and the total colloid content was no greater than 1.5% to 2.5%. Over 26% of the sand was retained in the 60 mesh sieve while another 50-60% was retained by the 140 mesh sieve. The moisture and xylene equivalents for the top 3.5 in. were 6.07% and 3.60% respectively.

Chemical analyses of the coastal plain soils indicate a very low level of fertility. This was shown by analyses of surface strata (top 4 in.) from the two Locations at Beaufort and from samples near Edgecombe and White Lake. The analyses were made at North Carolina State College by Mr. Robert Schramm, using standard colorimetric methods. Although the samples were taken from widely separated areas, they were markedly similar in chemical composition. The most noticeable characteristics of these soils are the high acidity (pH 3.5-4.9), the complete lack of detectable calcium, manganese and nitrate, the very low amounts of ammonia (2 ppm), iron (1 ppm), magnesium (1 ppm), and phosphate (less than 2 ppm). The concentration of potassium at Locations 1 and 2 was 2 ppm which is equivalent to an agricultural rating of "medium."

Loss on ignition tests were run on soil samples (0-4 in.) collected from numerous Dionaea sites. The average percentage loss was 8.79% for 33 sites.
with a range between 3.5 and 21.5%. Actually, most of the samples had less than this average loss and were remarkably similar. The high values were all due to the muck soils on which Dionaea is sometimes found.

SOIL MOISTURE

Moisture in the surface horizon of Dionaea zones is characteristic. Only during the late spring and summer do the better-drained soils, up slope from poecosis, dry to a depth of 2-4 in., but at other times, the water content is high at the surface and the soil is obviously wet within 9 in. of it (water table). The depth to this wet soil varies with the depth of the hardpan and the proximity to the poecosis edge, as was demonstrated by borings taken at intervals across the zones from the poecosis edge into the savannah at Locations 1 and 2. At the poecosis edge the depth to the water table averaged 6.5 in. while at the margin of the savannah it averaged 13 in. The hardpan at the poecosis edge occurred at an average depth of 13.5-19.0 in. and at the savannah 19.0-26.0 in. The average percentage of organic matter decreased with increased distance from the poecosis (13.75% at poecosis edge to 5.31% at edge of savannah). This is to be expected since runoff and drainage increase up the slope, resulting in better aeration and hence more complete oxidation of the organic matter.

During the summer of 1955 soil borings were taken at intervals (3, 8, 12 m and 2, 6, 10 m) along the slope from the poecosis at Locations 1 and 2 (Z1-Z3, Figs. 4 & 5) to determine the rate of loss and degree of depletion of soil moisture during extended periods of dry weather. Unfortunately, dry periods were infrequent and of short duration so that the longest period of observation without rain was 12 days. Only two relatively successful series of determinations were made: one over a period of a week immediately after a rainy period, the other over a period of 4 days after a week of dry weather. Rain terminated the observations for both series. Although it was thought that rain did not occur during these times, and the stations were visited twice a day during the apparently rainless periods, it is possible that the not uncommon highly local showers may have contributed to certain fluctuations which appear in the data.

To compare these soil moisture data from the field with the potential amounts held under defined tensions, determinations were made of soil moisture in undisturbed samples at \( \frac{1}{40}, \frac{1}{30}, 1, \) and 15 atmospheres pressure. The lower pressure determinations were made with a porous plate apparatus and the 15 atmosphere determination on a pressure membrane extractor.

Using the mechanically determined soil moisture values as a basis, the field data indicated that although the moisture content of the upper 2 in. of soil showed some fluctuation all along the transect, the greatest was at the outer (savannah) edge where, at times, the tension was considerably greater than 15 atmospheres. At the inner area of the zone the soil moisture tension rarely was higher than 15 atmospheres and in general remained around \( \frac{1}{30}-\frac{1}{40} \) atmosphere. The soils at the minus 4 in. level showed a much higher proportion of water, with nearly all of it being held at less than 1 atmosphere tension. Water is then readily available to the plant below the soil surface of the Dionaea zone if roots reach it. There is little apparent specific correlation, at least as determined in this study, between the amount of dry weather and depth of desiccation of the soil.

FIRE

 Burning plays an important role in the development of the sandy soils of the Atlantic coastal plain and thus in the ecology of Dionaea. Although fire does not reach an intensity great enough to ignite sub-surface organic matter (Garren 1943) it is strong enough to burn off partially any surface detritus and thus aid in its further decomposition. The usual type of fire in the southeast is shortlived on any area and passes over the ground rapidly, burning most of the low vegetation in its path but without heating the sub-surface soil very greatly. Below 1 in. very little or no change in temperature can be detected (Heyward 1938). Most areas where Dionaea is found are burned fairly frequently and thus an \( \Lambda_0 \) horizon is almost completely lacking and the humus is incorporated in the \( \Lambda_1 \) horizon. The resulting sparse ground cover of frequently burned areas permits rain to wash the surface layers clean leaving a pure white sand, but beneath, the sand is dark gray because of the added humus and burned organic matter.

No comparative tests were made in this study of the chemical characteristics of burned and unburned soils. Available information is rather contradictory (Garren 1943) but most of the evidence indicates that burning decreases acidity and increases nitrogen, replaceable calcium and organic matter. The soils tested had all been burned recently and thus if the generalization is true for burned, uncultivated soils, then the unburned soils must contain an even lower proportion of nutrients, which may possibly contribute to the disappearance of Dionaea from unburned areas. Heyward (1939) showed in his comparative studies of burned and unburned longleaf pine forests, that moisture content was decreased in the upper 2 in. of burned soils. The peaty soil surface around the edges of a poecosis, because of its higher water holding capacity, probably is less affected by fire and thus contains less burned material.

From the study of the soils which are found in the Dionaea region, it can be stated that these plants are usually found on a medium to fine sandy soil containing some organic matter, either incorporated as humus in a manner similar to grasslands, or as an accumulation of peat. The amounts of mineral nutrients are low, but possibly not as low as they would be in the absence of fire. The soils generally have a high water content which is due almost entirely to the high ground water table and the ease with which capillarity can supply the upper soil levels.
PLANT AND HABITAT

With the general nature of the habitat in mind, and particularly the physical factors involved, the field characteristics of Dionaea can be considered in relation to environment.

LOCAL DISTRIBUTION

As already pointed out Dionaea occurs in well-defined zones where changes in micro-relief are abrupt, and particularly this is true of the more northern habitats. Near Wilmington these zones or ecotones are much broader since the transitions between true pocosin and true savannah are commonly of far greater areal extent. Such wide zones are especially evident in Brunswick County between Wilmington and Southport, and in many of the large tracts of land belonging to the International Paper Company (especially in Pender and Horry Counties).

The relationship between slope and position of Dionaea in the field has already been referred to. A generalized diagram (Fig. 6) illustrates not only the change in the species composition up the slope, but also the change in peat, soil water, hardpan and organic matter relationships. Thus, it becomes clear that when the conditions of the zone containing Dionaea become more spread out, the plant will occupy wider areas.

Numbers of plants in the field vary widely. In some areas one is unable to walk without treading on them, while at other places they are so scattered as to be found only after careful search.

A plant census was made during the flowering season of 1956. Most of the data were collected at or near Location 1 and 2, but not within the designated study plots (Figs. 4 & 5). Counts were made of mature, immature and flowering plants on 20 randomly distributed plots 1 sq m in area (Table 1). Plants were distributed on the average of 89 per sq m, of which an average of 23 flowered. Throughout the study it appeared that flowering percentages of groups of plants were very low, and the census confirmed this observation, giving an average of 36-40% flowering for mature plants.

**Table 1. Censuses of flowering and non-flowering Dionaea plants in undisturbed natural areas.**

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<td></td>
<td></td>
<td>Mature flowering</td>
<td>Mature immature</td>
</tr>
<tr>
<td>1</td>
<td>11</td>
<td>920 (421 (40%)</td>
<td>218 (24%)</td>
</tr>
<tr>
<td>2</td>
<td>9</td>
<td>843 (321 (39%)</td>
<td>257 (30%)</td>
</tr>
</tbody>
</table>

EXTERNAL MORPHOLOGY

Although Dionaea has a complicated internal anatomy, its external morphology is relatively simple. It is made up of a short, unbranched, horizontal, white rhizome, surrounded by the fleshy bases of the leaves. The external form is that of an elongated bulb. From the lower surface arise 4-8 roots up to 15 cm in length. They are unbranched and bear long persistent root hairs. The rhizome lies in a slightly inclined position 2.5-4 cm below the soil surface, with the growing point at the lower end. The bilateral symmetry of the plant is masked by the radial arrangement of the leaves which is partly due to the way in which the youngest leaves ensheathe the growing point. Fully developed leaves may be either prostrate or upright, depending on the season.

The age of a naturally grown Dionaea plant cannot be accurately determined. Although inspection usually serves to distinguish mature from immature plants, mainly on the basis of number and size of the leaves, the conclusion may not be valid. Many mature plants may sometimes produce immature-type
leaves, especially if the growing point has been injured. Development from seedling to mature plant is slow, a period of probably more than 3 yrs being required for an individual to reach the flowering stage. There are no growth rings or comparable age indicators. The number of leaves plus the number of persistent dead leaf bases may give some indication of minimum age but the rate of leaf base decay varies with size. Another factor to be considered is rate of leaf production which fluctuates under different conditions. In general, mature plants have fewer and larger leaves (4-8) than immature (10-16).

HABITAT ASSOCIATES

Common associates of Dionaea have already been mentioned but it should be emphasized that, although several species do indicate the likelihood of a suitable habitat, none can be designated as a reliable indicator of its presence.

Plant cover in Dionaea zones is characteristically sparse. The soil surface is generally completely bare between the individual plants, although at the poecoosin edge Sphagnum is commonly present, forming dense matts. Vegetation is least abundant in the upper part of the zone and increases slightly from about the mid-point to the poecosin edge. Transects across typical margins (Figs. 4, 5) which were some 10 m wide showed only 26% cover in the upper 4 m with a slight increase to about 40% from the middle of the zone to the tall shrubs of the poecosin proper.

PHENOLOGY

Visible floral initiation is first apparent in the field early in April, and usually no further initials appear after the end of that month. Flowering begins about the last week in May and is usually over before the middle of June, although some plants may not finish before the beginning of July. Seed is usually ripe by the end of June, and dispersed by the middle of July. New seedlings first appear at the end of July and the beginning of August.

The terminal flower of an inflorescence always opens first and immediately begins shedding pollen although the stigma is still immature. Approximately 24 hrs later the stigma is receptive, but by this time most of the pollen has been shed. Individual flowers, of the 8-12 in an inflorescence, open at approximately 24-hr intervals. Laboratory evidence indicates strict cross-fertilization. Self-pollination experiments did not result in seed production in a single instance. It is to be noted that Ellis in his letter to Linnaeus suggested that his plants did not set seed because of insufficient temperature, but it seems apparent now, that cross pollination was not effected. Presumably, pollination in the field is entomophilous, apparently by various beetles, small flies and possibly spiders, all of which may be seen in the flowers. Plants usually have a single inflorescence but occasionally two or even three flowering stalks are produced.

Seed dispersal is probably by rain drop splash. The ovate seeds stand, with the larger end upright, partially embedded in the placenta and a force greater than that of ordinary wind or alighting insects is needed to dislodge them. Thus, it is postulated that the beating of rain on the seed heads is responsible. At the time of the year when seeds are ready for dispersal, convectional thunderstorms with violent rainfall are common.

The distance of dispersal from the parent plant is not great, usually not more than a few inches from the base of the stem, as is evidenced by the proximity of seedlings to the parent plant. However, dispersal could be extended by rain wash as the seeds are light enough to be carried in small streams of water which often form during rain storms. Very probably this explains the occasional concentration of plants along the high water marks of depressions in areas which otherwise contain few or no plants.

Seedlings are usually found in protected sites in the field, most commonly around the base of mature plants but often in Sphagnum matts as well. They do not occur in open areas on bare sand where they would be subject to battering by rain, or to desiccation resulting from high insolation. However, where the soil is bare, but sheltered by overhanging, taller vegetation and has a thin surface layer of fine semi-decayed plant remains and humus, satisfactory germination and development can take place. These conclusions were drawn from field observation and from field sowing experiments.

Although growth is slow, development may sometimes be surprisingly rapid. Plants from seed sown in the field in July showed an average of 5 leaves per plant (range 3-9) in October. The same number of leaves per plant were present again in January, although it must be realized that some of the original leaves had died and had been replaced by new ones. During this developmental period all the leaves were yellowish in color, only the glands on the inside of the traps being red. By the end of the first year presumptive seedlings usually have 8-16 leaves up to 1 cm in length. At the end of the second year, the number of leaves remains about the same but they may be 1.5 cm long. However, it is dangerous to generalize as some plants, known to be 1 yr old, show the same amount of development as 2-year-old plants. Fig. 7 (N and O) illustrates the typical shapes of young leaves.

Seasonal variation in the size, shape and color of the leaves is quite apparent in the field. In the early spring most of the plants are green with petioles up to 6 cm in length and traps about 2 cm long. The leaves may or may not be erect. Usually if there is any red coloration noticeable, it is limited to the glands of the inner surface of the traps. The petioles at this time have a width of about 1.5 cm at the broadest part. With the appearance of the floral axis, leaf initiation usually ceases and no new leaves are produced until after flowering. These new leaves show a marked difference in morphological characters—they have long narrow petioles (up to 12.5 cm) which are nearly or completely wingless, upright in orientation, and bear traps up to 3.25 cm in

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small traps (sometimes the leaves may be somewhat longer than is typical, Fig. 7H). However, during the summer, although the length of the leaves is equal to that of the spring type, they are generally prostrate, or slightly decumbent, and have petioles only slightly narrower than in the winter (Fig. 7J).

The shape of the individual trap is to some extent an indication of the maturity of the plant. Comparison of leaves of different ages indicates that besides the difference in the size of the traps (not a reliable guide) the general shape is different, the leaves of very young plants (Fig. 7N) being somewhat square in outline, while the leaves of older plants are almost reniform in shape (Fig. 7).

**DISCUSSION**

It is inferred from the climatic data that the climate is so similar within and beyond the range of Dionaea that, as such, it does not play a major role in delimiting the zonal areas or the overall boundaries of its occurrence. Nevertheless, the general climatic characteristics within the range play a very important part in the life history of Dionaea. The high summer rainfall is probably of great significance, since it tends to keep humidity high and thus to ameliorate drought conditions especially during germination which occurs in the hottest months. (Moisture content of the soil as shown later is an important influence in the seasonal changes in leaf morphology.)

The plant material produced in the savannah during the summer is still present the following spring, and as a result of low spring rainfall, dries out rapidly. This dead, dry material, being highly inflammable, is primarily responsible for the prevalence of fire at this time of year. Because fire appears to be of some importance in the occurrence of Dionaea and in maintaining favorable habitats, some attempts were made to clarify its effects. The results appear in the experimental section.

The chief differential climatic factor between the zones and the savannah is apparently wind as reflected in a differential moisture loss from atometer bulbs in the two sites. Hence, greater air movement in the open savannah must contribute to the faster drying of its surface soil.

One of the main factors delimiting the total range of Dionaea appears to be water. Comparison of field moisture determinations with the laboratory determined field capacity ($1/4$ or $1/2$ atmospheres) and the wilting percentage (15 atmospheres) shows that the top 2 in. of soil of the low inner margin of the zone rarely reached the wilting percentage, while soil at the outer margin often developed greater moisture tensions. Soil moisture tensions greater than 1 atmosphere seldom occurred at deeper levels. These determinations were made in the summer when possibly the soil does not dry out completely, so it is suggested that higher tensions may be developed during the spring. Thus it is likely that this season may impose the greatest limitation on the survival of
mature Dionaea at the outer boundary of the zone. Seedling tolerances are also important in the delimitation of the zone. The requirements for field germination are not generally met on the bare, highly insolated sand of the savannah and hence seedlings establishment is precluded.

The structure and composition of the soil (chiefly St. Johns Series) were shown by the analyses to be very uniform throughout the Dionaea range. The predominantly sandy nature of the soil together with the high proportion of surface organic matter and the proximity of the water table to the surface were characteristic wherever Dionaea was found. The limits of specific habitats of Dionaea appear to be due to local topographic differences resulting in alteration of soil and moisture relationships.

EXPERIMENTAL OBSERVATIONS

Field Experiments

Burning

It has already been indicated that fire may have a large influence on the growth rate of Dionaea in the field and on its survival in a particular area. Thus, certain experiments were carried out in the field to determine what effects of burning were most influential on plant growth.

Four series of plots (each 3 by 1 m) were spaced along lines traversing the Dionaea zone at Location 2 (Fig. 5) in July 1955. One plot in each series was at the edge of the pocosin and one at the edge of the savannah. Plots between were, presumably, representative of average Dionaea habitats. All surface vegetation was removed from 2 sq m of each plot and the refuse was collected and burned. The ashes and charcoal were reapplied to 1 sq m of the cleared portion of each plot after it had been burned over with a blow torch. A week later, Dionaea was transplanted from a nearby site into each section at the rate of 40 plants per cleared meter (one with ash, one without) and 20 per uncleared. The plants were marked with stakes and left, their further development being observed for the following 18 months.

Not until flowering occurred about 10 months later were the first obvious differences noted (Table 2). The plants in the cleared plots all flowered slightly earlier than in the uncleared or in the natural areas, and the flowering percentage in the cleared areas was higher (overall average on cleared, burned and unburned plots, 68%, uncleared plots, 51%). The figures for the burned and unburned plots are somewhat variable, but the overall averages show a higher percentage of flowering in the burned plots (72%) than in the unburned (64%).

The low figures for the uncleared plots are in general higher than those obtained in the natural areas (the average figure of the natural areas being 38% and for the uncleared plots 53%). The discrepancies in the figures which appear for the cleared areas, are unexplained, but the variation in cover and competition could be responsible, especially in the D plots (savannah). Here the plants in the uncleared sections of 4D and 6D (higher flowering percentage) had less competition than in the corresponding sections of 3D and 5D (lower flowering percentage).

After flowering, some differences became apparent between the paired sets of treatments on cleared portions of the plots. Those plants on the burned plots looked healthier, but the differences were of a qualitative nature and may have been caused by other factors. Although the responses in the experimental plots contributed no startling new information they do support observations made on burned areas elsewhere. Within 2 yrs after burning, plants in such areas are invariably more vigorous than plants in adjacent unburned areas.

Supplementary information on the effects of fire was gained by burning off all surface vegetation, including Dionaea, from undisturbed blocks of soil brought in from the field. Resulting temperatures did not kill the growing points of Dionaea, as new leaves appeared within 2 weeks after burning. The Dionaea plants in the blocks of soil treated in this manner showed visible floral axes earlier and were more vigorous than plants in similar unburned blocks. Thus, the stimulating effect of burning must either result from the release of nutrients into the soil in a more available form as suggested by Garren (1943), or it must be by reduction of competition. On the basis of the field experiments and observations, it appears that the latter is the more obvious explanation, but the nutrient angle cannot be neglected.

Although the rhizomes of Dionaea are in the top 2.5-4 cm of soil, the larger ones are well protected from fire injury, and the roots, being deeper, are unlikely to be affected. This may be deduced from the temperatures, recorded by Heyward (1938) for the soil heating effects of forest fires in longleaf pine areas. The surface soils of Dionaea zones being moister, the temperatures during burning are likely to be lower than those obtained in the longleaf soils.

Transplanting

The series of plots used for the burning experiments was also used to make other observations. A comparison was made of the size and vitality of the transplants within the normal range of the zone and at its extreme margins (Fig. 5).

There were several clear-cut differences in the vigor of the plants. Within the zone the diversity among plants was no greater than the individual variation to be expected in any population. However, the plants in the savannah (D plots) showed a distinct retardation in vegetative development in the spring of 1956. They were much more compact and less developed than those within the normal zone. The spring was moister than usual for the region, no fires occurred in the area of observation; the summer of 1956 was also wetter than usual, although no hurricanes occurred that year. Still, plants in the savannah plots had a mortality of 9%, compared with only 0.25% for those in all other plots. Had the spring and summer been drier, it is probable that the
mortality rate would have been higher, although the plants may have gone into a dormant condition.

Although the plants in the cleared plots flowered earlier than those in the uncleared plots, the savannah transplants flowered a little earlier than the rest of the plants in the transplant experiment. The flower stalks in general were shorter in the D plots than nearer the pocosin, with fewer flowers per inflorescence. It has already been noted that the plants in the uncleared D plots with greater competition showed lower flowering percentage than those in the lower-competition uncleared plots. However, in contrast, the low flowering groups (3D and 5D) were more vigorous (vegetatively) than the high flowering groups (4D and 6D), but all plants of the uncleared D plots were much more vigorous than those in the cleared D plots.

On the other hand, plants of the uncleared areas of the other plots were all smaller than in the cleared areas, and this difference was more noticeable the greater the intensity of shade and competition from over-hanging vegetation. Most of these shaded plants retained winter or spring leaves through the summer. In relation to water, the plants growing in micro-depressions were more vigorous than those on slight ridges, particularly in the drier plots. At the inner edge of the zone the effect of the greater amounts of water was mainly apparent in the type of leaves produced by the plants growing there: although up-right leaves were developed, in general they were winged. Plants of the drier areas produced narrow petioled summer-type leaves (Figs. 8 & 9).

Flowering of the plants of the inner plots (A and B plots) was greater in the cleared than the uncleared areas (Table 2).

One other plot, 0.5 m in width and 10 m in length running parallel with the transect plot containing Z3 at Location 2, was completely cleared of all vegetation except the flytraps, but the surface soil was left undisturbed. The important difference which appeared in this cleared plot was in the relative sizes of the plants. The largest plants were at the pocosin end, and in general, had the largest leaves and the longest flower stalks. Flowering percentage was higher throughout this plot than in natural areas.

An interesting confirmation of these transplant experiments was gained when a visit was paid in January 1957 to Mr. Aubrey Shaw of Lake Creek Community, Bladen County, who had transplanted Dionaea into several locations showing obvious physical differences from the natural habitat. The transplants were made in 1950 as follows:

1. Dry area
2. Heavily shaded area
3. Moist area
4. Shallow drainage trough (high pH)
5. Submerged in a pond.

1. The dry area was in an open cut-over longleaf pine savannah. The surface soil of this savannah becomes almost completely desiccated in summer, and, as a result, these transplants have two growth cycles during the year. It was reported that after the first surge of spring growth, the plants became completely dormant for the summer months, then produced new leaves toward the end of the summer or
the beginning of autumn after the heavier rains began. No flowers had been produced, the dormancy setting in about the time of initiation of the floral axis (April). The area where they were transplanted had several ridges and hollows; those plants in the slight hollows were more vigorous than those still alive on the ridges. Mortality had been heavy in this group of transplants. At the time of observation, all the plants in this area were small, green in color and in typical winter condition.

2. The shaded area was at the edge of a trail through a pocosin where the soil was very wet, and where leaf litter from the overhanging shrubs had built up a thick mat of semi-decayed mold. During the winter and probably during the summer as well, the plants are unable to produce leaves of sufficient length to penetrate the overlying litter. Only a few of these transplants had survived, and none had flowered. Their leaves were green, prostrate, broad-petioled, without traps and of a thin papery texture.

3. The moist area was in a position on higher ground than area 2, but close by, without the shade factor and with very little competition. These plants were very healthy, and had prostrate leaves of a deep red color and broad, very short petioles. Dead leaves gave evidence that some upright leaves had been produced during the summer. Flowering occurred in 80-90% of the plants in 1956, and a good crop of seedlings was present.

4. The shallow drainage trough, which originated in a cultivated field, was always wet but seldom carried a large volume of water. The soil was less acid (pH 5.5) than is normal (pH 3.8-4.5) in Dionaea habitats. The plants here were large and the leaves green, but the glands showed a slight red coloration. The leaves were more typical of the spring than the winter type, with long, winged petioles and medium-sized traps. The plants had flowered in 1956, and the seedlings were larger and relatively more abundant than in area 3. It was reported that the "catch rate" of these plants was relatively high, and many of the traps investigated showed the remains of partially digested beetles, woodlice and planarians.

5. The submerged plants had been completely under water for 7 yrs and were still very vigorous. At times the traps of some leaves had been above the water level, but the growing points and petioles had always been submerged. There had been no flowering during the time of submergence. All plants were in an extreme spring condition, displaying very long petioles (13-15 cm) and traps (4.25 cm). Planarians, mayfly and other aquatic larvae and even newts were seen in the traps in partially digested state. Most of the traps examined contained either newly trapped animals or the remains of digested ones. Thus, the trap mechanism is not only sensitive under water, but is able to close with sufficient rapidity to catch fast-moving aquatic animals.

Prior to the visit to Mr. Shaw, flooding experiments had already been completed in the greenhouse. Mature plants had been kept continuously flooded for 3 months without injury. Immature plants which had
been in water-logged soil for 7 months remained large and healthy, and some produced flowers. Soil conditions of the plants in Mr. Shaw's field area 4 and of those in the water-logged soil of the greenhouse were similar.

The plants in the natural areas of Lake Creek Community were similar to those in the drier parts of Locations 1 and 2. The flowering ratio, as far as could be determined, was similar to that in the study area, and seedlings were present. In one small region, the competitive vegetation had been kept at a minimum, and the plants here had produced more flowers than those under completely natural conditions. Fire had not occurred in the area for about 15 yrs, and this may partly account for the small size of most of the plants. Dionaea in this region was scattered over a wide area of semi-savannah, mainly at the edges of slight depressions containing a heavy growth of low erieeous shrubs.

SHADING

At Locations 1 and 2 in January 1956, 4 areas (containing a total of 188 mature plants) were shaded with layers of cheeseloth which reduced the light intensity by about 50%. About 40% of the plants developed obvious floral initials but an average of only 15% of the total number of plants flowered (7.6% at Location 1 and 23% at Location 2), indicating high mortality among these initials. No comparative counts were made of the dead initials in the natural areas because the observed scarcity did not appear to warrant it.

The floral axes of the shaded plants reaching maturity were badly bent, even though not touching the cheeseloth, and the flowers were atypical, malsor- ed and set no seeds. Most of the plants remained in winter or spring condition through the summer of 1956, and showed a more marked development of the winter condition in 1956-57. During the summer the plants were somewhat etiolated and prone to insect attack. It was readily observed, in all areas visited that, under heavy shade, plants did not produce as many flowers as in the open; this was substantiated in the transplant experiments already described.

FLOWERING

General observation suggested that flower production is not correlated with such morphological characters as size, and number of leaves. After apparent maturity, measurable characters appear to be equally distributed among flowering and non-flowering plants alike. Consequently, within Locations 1 (Z1) and 2 (Z2), flowering plants were staked in 1955 so as to be recognizable in 1956. These plants when counted the following year showed about the same proportion of flowers as in the wider census, the average being 40%. However, there was a considerable difference between the percentages at the two stations, the higher being at Location 2. This difference was also apparent in the shading experiments. Direct comparison with the wider census figures cannot be made as these were taken from a larger area than the designated stations.

The differences in the percentage of floral initiation and flowering at Locations 1 and 2 are possibly related to the occurrence of fire in these areas. Although fire had occurred in both areas in the spring of 1955, it appeared to have been more effective in burning surface vegetation at Location 2 than at Location 1.

One interesting fact emerges from these studies, namely, that although greenhouse (as reported later) and natural field populations show a low flowering percentage which is apparently not directly correlated with size, vigor, or the production of flowers the previous year, plants which were transplanted to cleared plots, or in areas from which the other vegetation had been removed, showed a considerably higher proportion of flowers. Absence of competition is not the only factor, or flowering in the greenhouse should have been in higher ratios.

DISCUSSION

The field experimental studies on Dionaea to a large extent were not conclusive but do point up important factors affecting the presence of Dionaea in local habitats. Fire has been shown to be important at least to the extent that it eliminates competition and thereafter allows more vigorous growth of Dionaea. The temperatures generated during surface fires are not injurious to mature plants. Although the leaves are killed, the rhizome is apparently unaffected and new leaves appear rapidly after fire.

 Burning also removes accumulated litter, which effectively excludes Dionaea from a site if it becomes too deep. Where the deep litter collects in wet areas, establishment of Dionaea is prevented.

Heavy shading reduces floral maturation, although apparently it does not affect floral initiation to any great extent. Thus, in areas where Dionaea has become established, elimination of fire and the consequent development of heavier growth of associated species will reduce flowering and hence, eventually, the population will become entirely eliminated. One example of such a phenomenon in progress is in an International Paper Company's loblolly plantation at Edgecombe. Evidently at the time of planting the pines, there was a large and vigorous population of Dionaea, but since then with protection from fire, the grasses (mainly Aristida) thrived and formed a very thick ground cover. This cover reduced floral maturation and the plants have lost vigor so that the Dionaea population will probably be seriously reduced or even eliminated over a large section of that area.

Another factor shown to be of importance in the production of floral initiations is the duration and time of the driest season as well as the extent to which the soil dries. Thus, although Dionaea can survive periods of severe desiccation by going into dormancy, floral production is prevented if the dry
period comes in spring, and germination and establishment of seedlings are prevented if the dry period comes in the late summer or fall. However, if sufficient organic matter is incorporated in the soil, allowing greater amounts of water to be held, and if the water table is sufficiently high, the effects of the dry period are considerably reduced.

**Laboratory Experiments**

**Water Relations**

Although determinations made during the summer show that the soil moisture of the Dionaea zone rarely falls to the permanent wilting percentage, there are times when soil moisture stress may be an important limiting factor at the outer limit of the zone. Thus it was considered desirable to determine the ability of Dionaea to dry out the soil and to withstand severe moisture stress.

Since the root system of Dionaea is poorly developed, and growth of the plants is slow, the conventional method of testing the permanent wilting percentage of the soil (PWP) was not followed. The root systems of mature plants were placed in glass tubes (4 in. long, 0.5 in. in diam.) and air dry A horizon St. Johns Series soil poured in. The base of the tube was covered with a double layer of cheesecloth to prevent loss of the soil and to allow drainage. The tubes were then immersed in water until the soil was saturated, and buried up to their necks in sand for 4 weeks to allow the plants to recover from transplanting. At this time the tops of the tubes were sealed with vaseline (around the base of the plant leaves) and the whole tube wrapped in aluminum foil to prevent loss of water by evaporation and possible light damage to the roots.

The experimental plants were left in a sunny position in the greenhouse and weighed each morning. Permanent wilting (youngest visible leaves were wilted in the morning) occurred within 2 weeks. Each plant was then removed from the tube and a soil sample taken from around the roots (roots removed) for determination of moisture percentage by oven drying. The experimental plants, consisting now only of rhizome and roots, were placed then in a favorable environment to recover.

To determine the availability of the water present in the soil used, when the plants wilted, a 15 atmosphere moisture determination was made with the pressure membrane extractor. A conventional determination of PWP of this soil was also made using sunflower. To insure growth of sunflower in St. Johns soil, the acidity was adjusted to pH 6.5 by the addition of calcium hydroxide.

Results indicate that both Dionaea and sunflower are able to dry out this soil below the mechanically determined 15 atmosphere tension (5.31%). The PWP of the soil using Dionaea as an indicator was 3.38%, and sunflower was 3.73%, but the difference between these two is probably not significant.

The amounts of moisture lost by Dionaea were highest at first (0.83 gm in first 2 days) but dropped off rapidly (0.192 gm on 6th day, 0.052 on 14th day). This rapid drop in moisture loss was probably caused first, by the loss of water from the soil immediately around the roots, and secondly, by the early wilting of mature leaves and cessation of growth by the immature leaves as a result of moisture stress. The very small amount of water loss just prior to PWP (0.052 gm) can be attributed to the almost complete elimination of the transpiring surfaces (due to permanent wilting and/or death of the mature leaves).

When, after severe desiccation, these plants were placed in a favorable environment, new leaves began to appear within 2 weeks and almost 100% recovery followed. Apparently sufficient reserve material is stored in the swollen leaf bases to provide for rapid new growth after the return of moist conditions.

Further confirmation of this type of reaction in Dionaea was found when a number of individually potted plants were sealed off to prevent any loss of moisture except through the leaves. After 2 months, signs of severe drought were apparent, growth had ceased and all leaves had died. However, several of the plants later initiated new growth, although no water was added. The plants showing this new growth survived for approximately 6 months; this second growth was very slow, and the new leaves were small and very leathery, without traps. When examined later, it was seen that only the largest rhizomes had produced the second growth. Mature plants are able to withstand several periods of alternating severe drought and good water conditions without going into dormancy, while immature plants will not survive.

Studies such as these, as well as the report of the dry transplant area of Mr. Shaw, suggest that the rhizome with its surrounding swollen leaf bases is extremely important in allowing Dionaea to withstand periods of extreme dryness.

**Soil Texture**

As already described, the native soil of the southeastern coastal plain is mainly sand with a certain amount of burned and unburned organic matter incorporated into it, is very acid and of low fertility. In investigating the range of tolerance of Dionaea to varying habitat conditions, different soils were used to determine their effects on general growth and flowering. Two experiments were designed, one using plants taken from the field not long before floral initiation occurred (March 1956), and the other using plants collected at the end of the summer (September 1956).

In the first experiment, 12 large, vigorous plants were transplanted into flats containing the following soils:

| Flat 1 | Natural coastal plain soil |
| Flat 2 | A local clay-loam garden soil |
| Flat 3 | A specially prepared greenhouse potting soil |
| Flat 4 | Washed white sand |
| Flat 5 | Pure peat moss |

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All flats were placed together in the greenhouse and watered with distilled water. Only 11 days elapsed before floral initiations were noticed and after the 23rd day no initials developed. The only instance where all plants developed visible initials were those in Flat 2, but 11 initials appeared in the plants of Flats 1, 4 and 5, and 7 in plants of Flat 3.

However, after initiation, responses varied. Within 30 days of transplanting, differences in the general leaf coloration and shape were apparent. In Flat 4 the traps began to develop a deep red color. Plants in Flats 1 and 2 showed the same trist but to a lesser degree, while the plants in Flats 3 and 5 remained green. These differences became more apparent with the development of deeper coloration in the traps of plants of Flats 1 and 4; only the glands became red in the plants of Flat 2, giving the traps a pinkish color; those in Flats 3 and 5 remained green, although the plants in Flat 5 were much darker than in Flat 3.

The floral initials, although appearing approximately at the same time, did not develop at the same rate and many did not reach maturity. After 41 days only one initiation was still alive in the greenhouse potting soil (Flat 3), and 3 of the plants had died. This remaining initial flowered 44 days after its appearance, but the flower stalk was extremely stunted, the stem twisted and bent, and the inflorescence poorly developed with only a few malformed flowers. Although the flowers of this inflorescence were crosspollinated, no seeds were set. Differences appeared in all the flats which could apparently be related to the soil type in which the plants were growing. The most prominent differences are summarized below:

Flat 1. Natural coastal plain soil: All plants bloomed within 49 days of their initiation, although 2 plants did not reach maturity owing to accidents with flowering shoots. After flowering, all plants developed normal summer-type leaves with the characteristic red coloration.

Flat 2. Local clay-loam garden soil: Flowers of 4 plants finally reached maturity within 46 days of floral initiation. Thereafter, the plants showed little vigor, the leaves remained very leathery and of the late winter type. In general, the leaves did not develop traps.

Flat 3. Greenhouse potting soil: One plant flowered within 44 days and died shortly thereafter. All other plants died within 70 days of the time of transplanting.

Flat 4. Washed white sand: All initiations reached maturity within 47 days. After flowering, vigorous growth occurred with the production of summer leaves and red coloration.

Flat 5. Pure peat moss: All initiations reached maturity within 48 days. After flowering, the plants remained in typical spring growth condition, with broad petioles and small traps.

Table 3 summarizes the development of the plants used in this experiment.

When the experiment was finally concluded after 5 months, all plants in Flats 1, 4 and 5 were alive and very vigorous although the plants in Flat 4 were much larger than those of the other two. In Flat 2 only two plants were still alive, and were very unthrifty. These were taken from the soil and the roots washed. The probable cause of their low vitality was immediately apparent—there had apparently been no new root growth during the whole time of the experiment. Each plant had 4 roots and not one was more than 4 cm long. In contrast, plants removed from the other flats, each had 6-8 well-developed roots which averaged 3-5 cm in length (in Flats 1 and 4), and 15-20 cm in length (in Flat 5).

This experiment indicates that soil differences do influence the rate and type of development of Dionaea. At first, the sudden rise in temperature from the field to the 72°F greenhouse was probably responsible for the speed of appearance of the initials without any affects from the soil itself. However, after a time, the health and vigor of the plants reflected the soil type, with a decline in those plants in pure mineral soil (possibly the speed of decline in Flat 3 was partially due to the fertilizer added in the preparation of that soil), which led to coloration changes, loss of initials, loss of fertility, and finally, death. The explanation appears to lie in the fact that root growth is suppressed in the heavier soils. The higher pH and nutrient content of the artificial soils are probably contributory.

A second experiment involved the use of different proportions of sand and clay as the substratum for
Dionaea. Transplants were made in September, 1956, and carried through to January, 1957. Mixtures of clay (Georgeville, a kaolinite type) (100%, 75%, 50%, 25%, 0% by volume) and sand were made and duplicate flats of each mixture prepared. Thirty mature Dionaea were planted in each flat as well as ten 2 to 3-yr-old plants.

Results of this experiment were unexpected, as the plants in the lower proportions of clay were as slow in growth as those in the higher, and generally died off more quickly. Georgeville clay has been shown to contain a high percentage of mineral nutrients, which may be the reason that all plants did poorly. The young plants all died within a month of planting, while plants in the flats with 25% and 50% clay had all died within 2 months. At the end of the experiment, only 10 plants were alive in the 100% flat, and 15 in the 75% flats. The plants in the sand flats all grew normally.

**NUTRIENT EXPERIMENTS**

Knowledge of the nutritional requirements of Dionaea would probably shed some light on the range of its habitat demands, and might provide a partial explanation of its endemism. Early investigators were intrigued with the problem of capture and digestion and Canby (1868) foreshadowed in his paper the nutrition work of Darwin which appeared in 1875. The following year, Balfour (1876) also published results of digestion experiments. Curtis (1834) had remarked, “It is not to be supposed that such food [insect] is necessary to the existence of the plant, but like compost, may increase its growth and vigor.” The other early workers had similar views, with Sachs (1887) suggesting that animal substance not only improved vigor, but those plants prevented from “feeding” remained small and did not flower. De Candolle (1876), on the basis of his work (6 week experimental period), concluded that absorption of animal material was unnecessary for normal development. Tate (1875) had already come to the same conclusion for Drosera.

In spite of all the discussion in the early literature, no definite conclusions can be drawn concerning the role of animal matter in the life cycle of Dionaea except that further investigation of nutritional responses is necessary. Consequently, preliminary studies of both the mineral and organic nutrition of these plants were begun.

Nutrient solutions (modified from Burkholder & Nickell 1949) and a dilute Honglands solution were the main mineral solutions used, and a yeast protein extract and Droso phila melanogaster were the sources of organic nutrient. The mineral solutions were supplied through the soil and through the leaves, and the organic material through the leaves only. Plants were grown in washed sand. The seedlings were germinated in the laboratory and the older plants were obtained in the field.

Details of the exploratory experiments would not be justified in view of the inconclusive results. The generalizations suggested by the work indicate that intensive study along these lines would yield rewarding information. All plants receiving mineral nutrients grew poorly, while all the controls (watered with distilled water) showed much more satisfactory growth. The mature experimental plants steadily declined in weight, and died after about 3 months. Growth of all plants whether experimental, control, or in normal soils of the coastal region, was very slow, and this fact prevented further experimental work in the time available. The plants which were “fed” organic material, on the other hand, showed more vigorous vegetative growth. None of the plants under the various nutritional regimes flowered in the season following the experiments, while approximately the same proportion (45%) of the control plants flowered as was noted in the field (40%). It is probable that poor growth of the experimental plants resulted from using too high a concentration or the wrong proportions of nutrients.

**FLOWERING**

The variability of flowering responses in several experiments and the fact that only about 40% of mature plants flower in the field indicated a need for study of possible influencing factors. Since floral initials were first apparent in the field in April, it was postulated that production of flower buds in Dionaea is a photoperiodic response. A supporting reason was that field studies, already reported, had indicated the importance of light intensity as a factor controlling development of floral initials.

To test this hypothesis, a combined light-intensity-photoperiod experiment was designed in which plants (collected from the field in early January 1956) were placed in daylengths of 24 (continuous light), 16, and 8 hrs. Temperature and humidity were controlled in the 24 hr regime, the former at 72°F and the latter at about 45%. Both the other regimes fluctuated according to the temperature and humidity of the building. Forty plants in each regime were exposed to a light intensity of 500 fc, and the 2 shorter regimes also had groups of 40 plants under light intensities of 1000-1100 fc and 50-100 fc. When the flowers opened, they were all artificially cross-pollinated (if pollen was available) by use of a camel-hair brush.

Not only did the times of appearance of the floral initials differ in the various groups, but also the final percentage of flowering (Table 4) and the general leaf morphology.

Within a month after starting the experiments, morphological changes were noticeable in leaves initiated after exposure to the new light regimes. Some of the changes were very gradual, requiring 4-6 months to attain the final type of leaf. In part this was probably due to the habitat from which the plant was taken and also to its maturity at the time of transference. Figure 7 shows the early types of leaves produced and the final types, if these were
markedly different. Descriptions are given separately for each daylength regime.

1. The 24-hour photoperiod (Fig. 7G). (500 fc only). Leaf type stabilized rapidly to typical open field, summer form; petioles all wingless, some long, some short; traps generally larger and deep red (spines, glands, leaf tissue), color often extending on to petiole; some plants (long or short-petioled) devoid of red color, were usually yellow green as also observed in the field—possibly genetic or due to nitrogen deficiency. All plants developing visible initials (32%) produced flowers and viable seed when pollen was available for cross-pollination. (Fig. 10, #308 shows flowering plant before typical leaf type developed).

<table>
<thead>
<tr>
<th>Day-Length (hrs)</th>
<th>Light Intensity (f. c.)</th>
<th>Number Plants</th>
<th>Number Initiating</th>
<th>Number Flowering</th>
<th>Initiation Dates</th>
<th>Average Days Till Flowering</th>
<th>% Flowering</th>
<th>Seed Set</th>
</tr>
</thead>
<tbody>
<tr>
<td>24</td>
<td>500</td>
<td>50</td>
<td>16</td>
<td>16</td>
<td>16 Feb 26</td>
<td>56</td>
<td>32</td>
<td>+</td>
</tr>
<tr>
<td>16</td>
<td>1000-1100</td>
<td>40</td>
<td>17</td>
<td>16</td>
<td>25 Feb 13 Mar</td>
<td>27</td>
<td>40</td>
<td>+</td>
</tr>
<tr>
<td>16</td>
<td>500</td>
<td>40</td>
<td>6</td>
<td>3</td>
<td>29 Feb 13 Mar</td>
<td>37</td>
<td>8</td>
<td>+</td>
</tr>
<tr>
<td>16</td>
<td>50-100</td>
<td>40</td>
<td>11</td>
<td>2</td>
<td>7 Mar 17</td>
<td>45</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>8</td>
<td>1000-1100</td>
<td>40</td>
<td>5</td>
<td>5</td>
<td>26 Feb 11 Aug</td>
<td>32</td>
<td>13</td>
<td>+</td>
</tr>
<tr>
<td>8</td>
<td>500</td>
<td>40</td>
<td>3</td>
<td>3</td>
<td>21 Feb 10 July</td>
<td>39</td>
<td>8</td>
<td>+</td>
</tr>
<tr>
<td>8</td>
<td>50-100</td>
<td>40</td>
<td>4</td>
<td>1</td>
<td>28 Jan 6 Mar</td>
<td>60</td>
<td>2</td>
<td>0</td>
</tr>
</tbody>
</table>

#576); only 5% of plants flowered while 28% produced initials. Deformities noted in stamens, pistils and petals; only 2-3 flowers opened per inflorescence; no seed set.

![Fig. 10. Plants grown under medium light intensity (500 fc). #516—8-hr photoperiod, note short flower stalk and short, broad-petioled leaves. #368—16-hr photoperiod, floral axis elongate, upright, spring-type leaves. #308—24-hr photoperiod, leaves long but prostrate (spring-type), traps intensely red. The short floral axis doubled its length before flowers opened.](image)

2. The 16-hour photoperiod. Stabilization of leaf type slower in all regimes than under 24-hr light.

50-100 fc (Fig. 7D). Leaves thin, prostrate, papery, green; petioles long (9 cm), medium wide (1-1.5 cm) with wing tapering to base; traps small; floral axes attenuated, weak (Fig. 11, #576). Leaves in early phase of heart-shape eventually produced; long, attenuated floral axis typical.

500 fc (Fig. 7E). Leaves in summer months generally erect, petioles long; traps medium size, somewhat leathery, glands red, intermediate tissues green giving traps pinkish tinge, darkening toward midrib (Fig. 10, #368) (Leaves similar to shaded, spring field leaves). During winter, leaves generally prostrate, no red color, petiole wings slightly wider; flower stalks long, well-developed, upright (Fig. 10, #368); 15% produced visible initials of which 50% flowered; viable seeds were set.

1000-1100 fc (Fig. 7F). Leaves identical with those of 24-hr regime, leathery, narrow—petioled (0.5 cm). (Fig. 12 shows several plants with varying leaf types, all except #374 eventually produced upright leaves). Leaves produced during winter months typical of spring field type—no red coloration and less leathery; flower stalks...
and flower heads well developed, 40% of plants initiated and flowered, all set viable seed.

3. The 8-hour photoperiod. Leaf type fairly slow to stabilize and almost totalt distinct from plants of other regimes.

50-100 fc (Fig. 7A). At first some leaves (Fig. 13) similar to those under higher light intensities of same day length but within 5 months, leaves typically long (6 cm), prostrate, dark green, thin and papery; traps small or represented by a “beak” of undifferentiated tissue at end of petiole. (Fig. 11, #568 leaves at intermediate stage in course of development). Flower stalks attenuated, 2% flowered although 10% produced visible initials; stamens and petals malformed, pistil poorly developed. No seed set.

500-fc (Fig. 7B). Leaves short (4-5 cm), leathery, intense dark green, prostrate with heart-shaped petioles and medium-sized traps (1.5 cm) (Fig. 14); no red color at any time. Floral axes short and thick, flowers well developed (Fig. 10, #316). All plants with visible initials (8%) developed flowers and viable seed.

1000-1100 fc (Fig. 7C). Leaves short, leathery, light green (glands slightly red), wide petioled (Fig. 15); traps (1.25 cm) shorter than under 500 fc; floral axes short, compact (Fig. 16); all plants with visible initials (13%) produced flowers and viable seed. Some of these 13% developed 2 or 3 different flowering axes during the summer, a phenomenon which is only occasionally observed in the field.

Transference of plants from one regime to another resulted in the production of leaf types characteristic of the new regime, the rate varying with the amount of change involved. Fastest response was always noted when the plants were put into the 24-hr regime (red color developed within 2 wks), probably because of the controlled temperature and humidity. However, floral initiation was never effected in uninitiated plants when transferred from one regime to another, whether from field or green-

Fig. 12. Plants grown under high light intensity (1000-1100 fc) and 16-hr day. #542—typical summer type narrow-petioled leaves as eventually produced by all these plants; deep red traps of #374 typical but color develops gradually as leaves mature.

Fig. 13. Plant growth under low light intensity (50-100 fc) and 8-hr day. Typical of first leaves under low light, later traps are smaller and tissues less firm.

Fig. 14. Plant grown under medium light intensity (500 fc) and 8-hr day. Typical leaves are short, wide-petioled and no red color in traps which are relatively large.

Fig. 15. Plant grown under high light intensity (1000-1100 fc), 8-hr day. Leaves short, petioles relatively wide, color only at base of trap lobes.
Fig. 16. Plant grown under high light intensity (1000-1100 ft.). #15—8 hr day. Short, stout flower stalk, characteristic. #342—16 hr day. Traps deep red, leaves eventually all narrow-petioled, upright.

house (at a time when other plants in the group had visible initials) to controlled illumination or from one light condition to another. The controlled conditions provided did not result in floral initiation in any of these plants even after 13 months (second season) of exposure, regardless of their behaviour in the first season.

Several groups of plants were kept in cold storage (40°F) in both light (12 hrs) and total darkness for periods up to 3 wks, at different times of the year. Subsequent treatments were varied but again none was effective in producing visible development of floral initials.

It is realized that many of these treatments could have resulted in floral initiation, but subsequent development of these initials may have been arrested before they were macroscopically apparent. Also, many of the plants brought in from the field in January could have had floral primordia already present, and the increase in temperature in the greenhouse or the change of photoperiod could have been responsible for the early appearance of the initials.

Because it is well known that the carbohydrate-nitrogen ratio in some plants may control their flowering and fruiting (Kraus & Kraybill 1918, Hooker 1920) it is possible that an imbalance of carbohydrate-nitrogen in Dionaea might inhibit flowering production, even after floral initials had been laid down. Shading with cheesecloth reduced the usual 40% field flowering substantially even though visible initials were present in normal numbers. In low light intensity daylength experiments the floral initials failed to develop. In both instances the plants could have been strongly carbohydrate deficient. Under open, natural conditions the soils never showed more than 2 ppm NH4 and here a high or low supply of animal protein to the traps could likewise affect the balance and reduce the flowering percentages. In natural habitats, under normal illumination, too high a proportion of nitrogen produces rank growth and prevents development of floral axes. On the other hand, a nitrogen deficiency, compared with the amount of carbohydrate present, results in less vigorous growth, and, again, no flowering. On the basis of general observation it is more likely that plants in the field are mildly carbohydrate deficient than nitrogen deficient.

In the photoperiod experiments the yellow leaves under 24 hr high light intensity suggest nitrogen deficiency while under low light, the clad leaf type and floral initials that did not abort until almost mature suggest carbohydrate shortage (Fig. 11, #568).

Of the 42 plants which flowered in the greenhouse in 1955 only 10 flowered in 1956. This bears out what was found in the field, where only 40% of the plants marked as flowering in 1955, flowered again in 1956. However, by April 1957, none of the plants which had been in the greenhouse or laboratory since flowering in 1956, had produced visible flower buds.

These examples and the variability in time required for appearance of initials and flowers under different light intensities (Table 4) indicate that the requirements for floral development are extremely critical and effective only in a very narrow range. This being true, the low percentage of flowering of Dionaea in the field and in laboratory experiments is understandable.

Setting of seeds in Dionaea is somewhat differently related to light. Response to heavy shading in the field and to low light intensity with 8 and 16 hr days is similar to that of strawberry (Darrow 1927). Stamens, petals, and pistils of Dionaea are generally malformed. Thus, fruit formation is inhibited by floral deformities and no seeds are produced. Some plants, such as tomato, will flower under conditions of mild carbohydrate deficiency, but it is unlikely that this explanation applies to Dionaea because its plants, under heavy shade, do not show the rank vegetative growth usually associated with mild carbohydrate deficiency. Thus, although initially the carbohydrate and nitrogen content of some shaded plants may be appropriate for flowering, the shade conditions effectively prevent seed setting by causing malformation of both sexual and vegetative floral parts.

Although floral initials appear in field grown plants in early April, it is likely they are laid down much earlier, as is evidenced by their rapid appearance when field plants are brought into the greenhouse at earlier dates. Age of the plants is one factor which is involved in production of floral initials. Only mature Dionaea plants develop visible floral initials and this probably does not occur until they are more than 3 yrs old. Because the floral axis is terminal, its initiation prevents production of leaf initials until a new vegetative growing point is established. The new leaves which appear during floral development are obviously derived from leaf initials already present before floral primordia were laid down. The time lapse between the production of a leaf primordium and its appearance as a leaf initial is not known. Although floral primordia may
be laid down early and thus terminate new leaf production, observations were inadequate for generalizations. However, it was noted that in the number of individual plants, leaf production ceased for no apparent reason, to be renewed again after about a month. In these instances no floral initials appeared but this phenomenon could possibly be explained by assuming that during this time floral primordia were laid down but failed to develop. It is not known what combination of environmental factors is necessary to produce floral induction.

**Germination**

Immediately after field-ripened seeds became available in the summer of 1955, germination tests showed them to be approximately 70% viable. Consequently, ripe seeds were stored at room temperature for further experiments in the fall. However, when tested again in September no germination occurred, and thus the problem of the length of viability arose.

The next spring, seeds were harvested as soon as they ripened in the greenhouse and the collections from different plants were stored separately. Experiments were then begun to test the germination percentage and the length of viability after different treatments and various storage periods by the following procedures:

1. Seed was considered ripe when exposed after the capsule had turned black and had ruptured. Some seed was collected immediately, and some was left on the plant for a definite length of time before collection.
2. After collection, the seeds were counted and stored in glass tubes at 72°F.
3. At predetermined intervals seed was set out to germinate on damp filter paper in covered petri plates. All temperatures were controlled at 72°F under a photo-period of 12 hrs.
4. All seed was watered with distilled water. When the seeds had germinated and the seedlings were of sufficient size they were transferred to leached sand and watered with distilled water. It was from these that plants for the seedling nutrient experiment were taken.

Seed was set out to germinate at different time intervals after collection, at the rate of 10 seeds per test. Records were kept of the time of setting out and the time of germination, i.e., when the radical was first apparent. As the experiments progressed it became clear that there was no apparent after-ripening effect of the plant on the seed, once the capsule had opened.

After storage at 72°F for up to 4 weeks, half of each set of seeds was packaged in filter paper, layered in sand, and stored in the refrigerator (36°F) so that comparison could be made between cold storage and storage at normal temperatures.

Germination of unlayered seed averaged 87% for the first 40 days and 56% for the next 60 days (Table 5). After 100 days viability dropped to about 2% and after 140 days no germination occurred.

**Table 5. Germination of unlayered seed.**

<table>
<thead>
<tr>
<th>No. of Replicates (sets of 10 seeds)</th>
<th>Average Time (days)</th>
<th>% Germination</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Age (days)</td>
<td>To first seed</td>
</tr>
<tr>
<td>8</td>
<td>0-2</td>
<td>14</td>
</tr>
<tr>
<td>7</td>
<td>2-4</td>
<td>18</td>
</tr>
<tr>
<td>15</td>
<td>5-9</td>
<td>15</td>
</tr>
<tr>
<td>8</td>
<td>10-14</td>
<td>12</td>
</tr>
<tr>
<td>6</td>
<td>15-20</td>
<td>11</td>
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<tr>
<td>10</td>
<td>20-29</td>
<td>14</td>
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<tr>
<td>5</td>
<td>30-39</td>
<td>14</td>
</tr>
<tr>
<td>5</td>
<td>40-49</td>
<td>10</td>
</tr>
<tr>
<td>8</td>
<td>60-79</td>
<td>22</td>
</tr>
<tr>
<td>11</td>
<td>80-99</td>
<td>23</td>
</tr>
<tr>
<td>11</td>
<td>100-139</td>
<td>19</td>
</tr>
<tr>
<td>15</td>
<td>140+</td>
<td></td>
</tr>
</tbody>
</table>

The time from setting out to the first germination of seed in a set varied somewhat, but over the whole time it averaged 16 days for unlayered seed and 11 days for layered. The time lag between the first seed germinating in a set and the last, also fluctuated, averaging 25 days for unlayered seed and 20 days for layered seed. As the unlayered seed aged, some increase in the average time lapse was noticed between setting out and germination, although this may be more apparent than real. (Table 6). No seed germinated when older than 126 days at the time of setting out, but some few seeds, which were set out within 2 weeks of ripening, were up to 145 days in age before they germinated. No unlayered seeds over this age were viable and viability at this age was extremely rare (Table 5).

**Table 6. Germination of layered seed.**

<table>
<thead>
<tr>
<th>Date of Laboratory</th>
<th>averaged Time (days)</th>
<th>% Germination</th>
</tr>
</thead>
<tbody>
<tr>
<td>Collection Layering Setting out</td>
<td>First seed Last seed</td>
<td></td>
</tr>
<tr>
<td>April</td>
<td>June</td>
<td>July-Oct</td>
</tr>
<tr>
<td>June</td>
<td>14</td>
<td>Field</td>
</tr>
</tbody>
</table>

After layering, the percentage of germination remained high over the entire period of investigation. After 9 months, seeds were still showing 86% germination, equal to the average germination of up to 40 days for unlayered seed. The average over the whole 9 months period was 87%. Other differences have already been mentioned.

This difference in viability between layered and unlayered seeds is possibly explained by the presence of some metabolic mechanism within the seeds which is slowed down or completely stopped at low temperatures. Whether there is some production of autoxins or other products in unlayered seed, is unknown. Water and alcohol extracts, made from inviable seed and evaporated down to dryness on the filter paper which was used to germinate viable seed,
had a slight retarding effect on germination, but the final percentages were equal to the controls.

Thus there is a mechanism within the seeds which ensures germination immediately after ripening at which time field-formed seed show approximately 70-75% germination (slightly lower than laboratory seed). After 40 days, germination is down to 66% and after 100 days it is negligible. Thus germination is insured in the field at that time of year when rainfall, humidity and temperature are high. Optimum temperature and light requirements for germination were not determined although it has been indicated that the seeds germinated equally well in darkness or light. No definitive tests were made to determine whether viability of unlayered seeds was increased by storage in darkness. High humidity is necessary for the survival of the seedlings after germination; seedlings show a marked intolerance even to short periods of low humidity, although with age this intolerance decreases somewhat. Thus the early germination in late summer, insures that the seedlings will be established in the field before winter sets in.

**DISCUSSION**

The laboratory experimental work to a large degree confirmed many of the generalizations and deductions drawn from observation in the field. It is well established that mature Dionaea plants survive desiccation over short or even extensive periods of time, either by reduction of leaf area and production of leathery tissues, or in severe conditions by going into dormancy. However, seedlings cannot become established in areas where soil drought is common.

Factors related to soil are certainly important in determining the occurrence of Dionaea. Presence of organic matter is favorable because it helps maintain a high moisture content. Clayey soils do not support Dionaea possibly because of too high a proportion of mineral nutrients, as suggested by nutrition studies, and perhaps also because of mechanical resistance as indicated by the absence or reduction of root growth in all experimental soils except sand or peat moss.

Light intensity, moisture supply and photoperiod all influence to some degree the shape and size of the leaves of Dionaea. Low light intensities result in broad-petioled leaves both in the field and the laboratory. However, moisture supply also influences width of petioles, for plants in full sunlight have broader petioles in moist habitats than in relatively dry sites. Whereas moisture and light intensity may each condition plants to produce specific leaf characteristics, length of day can modify these responses under experimental conditions. In general, under long photoperiods elongated leaves are produced and short photoperiods given short leaves. Thus, the seasonal changes in leaf morphology noted in the field are explainable for, in summer, all leaves tend to be long and with the short days of winter, all leaves tend to be short. Within this pattern, the leaves are widest wherever light intensity is reduced and wherever there is an excess of soil moisture at a given light intensity.

Insect material, digested and absorbed through the leaves, results in healthier, more vigorous plants than controls without the insects. The question of the need for insects is still unanswered but the feeding experiments indicated that high rates of insect feeding result in either a failure of the development of floral initials or failure of their production. These greenhouse experiments were done under light intensities much lower than in the field. It is possible therefore, that the rate of insect feeding was too high for the amount of photosynthesis occurring and that these plants may have had a carbohydrate deficiency. It may be that a very critical carbohydrate-nitrogen balance in Dionaea is necessary for complete development of floral initials. If this balance is easily upset the nonproduction of flowers in the experiments and under some field conditions is explainable.

Heavy shading affects the development of the flowers, resulting in abnormalities of stamens and pistils and possibly the pollen itself. Seed is not set under intensely shaded conditions in the laboratory if the flowers do come to maturity.

Germination experiments showed that the seeds, stored under normal conditions, have only a short period of viability although layering in sand under cold conditions will lengthen the time apparently indefinitely. The mechanism responsible for the short viability is not known.

**DIONAEA MUSCIPULA IN ITS ENVIRONMENT**

Dionaea muscipula is endemic to the coastal plain of the Carolinas and within this area is almost exclusively limited to the St. Johns' soil series. The general climate of the region does not appear to be a major factor in the delimitation of the boundary of the range. Dionaea has specific requirements which must be met before populations can be established. It is found mainly in restricted zones between true savannah and true pocosin but where this ecotonal area is very broad, as in semi-pocosin or semi-savannah, Dionaea may be found intermittently throughout. Depth of the ground water table, soil surface characteristics, nutrient level, light intensity and fire appear to be the most important factor in delimiting populations.

St. Johns' series soils have a high water table and an organic hardpan which is usually not more than 24 in. below the soil surface in Dionaea areas. The soil is acid with a pH range of 3.9-4.5. Although Dionaea will survive in less acid soils, growth above pH 6.5 is poor. With increasing distance from the pocosin edge the water table is further beneath the soil surface. This results in accelerated decay of organic matter, and therefore less accumulation of humus in the surface horizons. Near the pocosin, oxidation proceeds more slowly and a thin layer of incorporated organic matter accumulates at the surface. Thus in spring and summer, depth to which the soil will dry out is greater with increased distance...
from the pocosin. Dionaea can survive but does not reproduce where water is seasonally out of range of the roots.

Dionaea is a light-demanding species but also requires a high water supply. Affecting the rate at which this plant is supplied with water is its root system, made up of 4-8 short, unbranched roots. Thus where the soil dries out below 2-3 in. in summer, roots cannot supply the plants with sufficient moisture. It is at such times that large plants with abundant stench reserve become dormant but small plants are killed.

At the pocosin edge, shrub vegetation is usually very dense and in such positions Dionaea may survive, but as flowering and seed setting do not occur under low light intensities, probably as a result of a critical carbohydrate-nitrogen requirement, satisfactory reproduction is not accomplished.

Seeds are ripe in June and July and field germination is first apparent at the end of July. The seed is viable only for a short length of time and in the field desiccation probably shortens it even more. Germination and development of the seedling occurs only in protected areas within the ecotone. High insolation and heavy rainfall which occur during the summer cause death of seedlings in unprotected sites by desiccation and battering. Therefore, the ability of seedlings to become established in an area is largely determined by the type of surface soil and the amount of protective vegetation.

Influencing the type of vegetation developed around a pocosin is fire. Where it is common, the ecotone has a relatively sparse ground cover made up of both savannah and pocosin species which are tolerant to differences in water supply. Where fire has not been a factor, dense ground cover is present. Only in areas of sparse vegetation cover will Dionaea be found in abundance and in a vigorous condition. Dionaea is fire tolerant. Growth and general vigor even appear to be stimulated by fire both by elimination of competition and by the effect on the plant itself.

Nutrient requirements are very low. The sandy coastal plain soils are very infertile and when Dionaea is transplanted into heavy soils containing abundant nutrients, growth is poor and death usually ensues. Part of the reaction of Dionaea to heavy soils may be due to its mechanical influence as root elongation is apparently impeded. Therefore, it can be concluded that the boundaries of populations of Dionaea are determined by the amount of moisture available to the plant, and the light intensity of the area. Fire influences the latter factor. The total range appears to be determined by the gross soil characteristics such as acidity, nutrient content and texture. Whether Dionaea is extending its range or not is a moot point. The period of seed viability is very short and dispersal is slow, and both of these characteristics would tend to prevent rapid migration. However, it seems apparent that wherever conditions remain favorable for Dionaea in areas which it now occupies, populations are in no danger of annihilation.

SUMMARY

1. *Dionaea muscipula* was first reported from Brunswick, North Carolina by Governor Dobbs in 1759. John Bartram sent the first dried material to England where it was examined and described by Ellis in a letter to Linnaeus in 1760 (published 1770) after he had seen living material brought over by William Young in 1768.

2. The numerous early investigators were primarily concerned with the nature of leaf structure and action. The relation of the plant to its environment, and its ranges in tolerances were almost completely neglected.

3. The maximum substantiated range of Dionaea extends from Chocowinity, Beaufort County, North Carolina, south to the Santee River, South Carolina and westward to the Moore County sandhills area. Although apparently not “doomed to extinction,” human interference limits its occurrence in some areas.

4. Inference from the geological history of the coastal plain suggests that the possible center of dispersal of the present distribution was the Moore County sandhills area from populations postulated to have been present there in pre-Pleistocene times. It is suggested that water has been the main dispersing agent.

5. General climate within the range is not significantly different from that 50 mi. outside, and is not considered a major influence in the delimitation of the boundary.

6. Topography of the coastal plain is level, and as a result, one of the main influencing factors on the development of soils from the sandy parent materials has been the height of the water table. Dionaea is almost exclusively confined to the St. Johns’ soil series which is predominantly sand, has a high water table, an organic hardpan, a thin surface layer of black incorporated organic matter, is acid in reaction and very infertile.

7. Pocosins and savannahs are two morphologically distinct vegetation types of the coastal plain, developed primarily as a result of slight differences in elevation and hence differences in the depth of the water table which affects the soil type. A gradient in vegetation and soil profile exists between them and in this ecotonal position Dionaea is normally found.

8. Dionaea is a light-demanding species but also requires a high water supply. Thus the savannah boundary of the Dionaea population is established by the depth to which the surface soil dries for this in turn influences the amount of organic matter present in the surface soil and the water supply in summer. The pocosin boundary is established by the density of overhanging vegetation.

9. Flowering and seed setting do not occur under low light intensities. Although Dionaea is able to survive under heavy shade, satisfactory reproduction
does not occur. It is probable that Dionaea has a high minimum light requirement for photosynthesis and that its flowering depends upon a very critical carbohydrate-nitrogen balance.

10. Fire is a very important factor influencing the density of vegetation in the savannah-savosin ecotone. Without this factor heavy ground vegetation is developed which would eventually eliminate Dionaea populations.

11. As for external morphology, Dionaea has a bulbous rhizome formed from overlapping leaf bases containing high starch reserves. The flowering axis is terminal, necessitating a new adventitious bud for continued vegetative growth. The root system is made up of a few short unbranched roots possessing long, persistent root hairs. The leaves arise from one end of the rhizome and appear as a rosette. Two main types of leaves are formed: winter-type—short, broad petioled and prostrate and summer-type—long, narrow-petioled and upright. Spring leaves are intermediate. Leaves produced under shade show a variation of form—are thinner in texture and always broad-petioled.

12. Photoperiod is the main factor influencing leaf length, and light intensity the main factor influencing petiole width. Thus under short photoperiods short leaves are produced and under long photoperiods, long leaves. A decrease in light intensity brings about an increase in petiole width. Under a given light intensity excess soil moisture may increase petiole width slightly.

13. Dionaea is fire resistant and after burning is usually one of the first plants to show renewed growth apparently because the sheathing leaf bases protect the growing point. Other surface-rooted plants are destroyed by frequent fires while Dionaea appears to be invigorated. If the growing point is injured, adventitious budding from the leaf bases will occur in well-developed plants.

14. No associated species can be designated with confidence as Dionaea indicators, since they vary from one site to another, are mostly tolerant of a wide moisture range and are typical of either savannah or savosin.

15. Well-developed Dionaea plants survive prolonged periods of drought by going into dormancy. Drought conditions may result in two cycles of growth following total dormancy in a single summer. Well-developed Dionaea will also survive prolonged periods of submergence under water. Neither submerged or drought-dormant plants produce flowers and seedlings will not survive under either condition.

16. Germination of fresh seed takes place within 10-21 days after placing in the germinator while after 100 days storage, germination is negligible unless the seed is layered in cold storage. Thus, field germination necessarily occurs in summer (July and August) because viable seed are not available in spring. Therefore, the significance of suitable soil surface (light humus on the sand) and protective vegetation is understood, as the physical environmental conditions would otherwise prevent seedling establishment. Development of seedlings is slow—after 12 months the diameter of the leaf rosette rarely exceeds 2 cm.

17. No criteria could be determined for estimating the age of these plants. Differences in leaf type and structure are apparent between young and adult plants. Mature plants are those considered to be capable of producing flowers and having large well-developed rhizomes. Flowering of seed-grown plants probably does not occur for at least 3 yrs. Flowering of plants from adventitious buds, developed on mature vegetative tissues, may occur within 12 months.

18. It is concluded on the basis of this investigation that the total range of Dionaea is probably determined by the soil type. Boundaries of local populations appear to be determined by the depth to which the surface soil dries out in dry periods and the light intensity. Seed viability, dissemination, and germination requirements determine the extent to which the plant can colonize new areas. Within well-established populations the frequency of fire chiefly determines the vigor and survival of the plants. Apparently the total range is stable at present and existent populations should survive except in areas where human activities alter the basic requirements of a suitable habitat.

LITERATURE CITED


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